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Hybridisation Experiments with *Thera variata*, Schiff., and *T. obeliscata*, Hb. (with Plate I. *).

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In my paper in the *Record* of March, 1926, I described my attempt to hybridise these two species in the autumn of 1925 and stated my intention to try again with the spring brood. With this object I went to the New Forest at Easter and beat about 350 *Thera* larvae from Douglas fir. Some were pupating before my return, and I found it impossible to separate those with pink legs from those with green ones owing to the lack of time, and so was unable to confirm my conclusion that the colour of the legs is a safe character, by which these two species can be differentiated. From the larvae with pink legs, which appeared to be more numerous, I expected to obtain *obeliscata*, and actually did breed rather more of this species than of *variata*. I had originally intended to cross the *variata* with *obeliscata* from Oxshott, but beating there was most unsuccessful and I only got one larva.

To avoid any risk of pairing between members of the same species, I separated my pupae roughly into males and females and rejected any imago, which had been with a member of the opposite sex of its own species for however short a time. Fortunately the sorting was satisfactory and very few were wasted for this reason. On April 25th, the first specimens of each emerged and the experiment was begun. To obtain pairings I had a number of boxes and into each I put two or three males of the one species with two or three females of the other. Imagines continued to emerge until May 27th, and, although parasites had destroyed more than half the larvae, there were quite enough for my purpose. On the whole *variata* appears to be a little later than *obeliscata*. By May 6th, I had many females of the latter but only three of the former, and the last imago of all was a *variata*. In order to make sure that I had not introduced a pair of the same species in any of the boxes the insects in each were examined at least twice and a final examination was made when they died. Altogether I used 33

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mules and 26 females of *obeliscata* and 32 males and 21 females of *variata*, and from these I got two fertile pairings of *variata* ♂ × *obeliscata* ♀ yielding 81 eggs, and five or six fertile pairings of *obeliscata* ♂ × *variata* ♀ yielded 200 eggs, the latter being the cross I failed to obtain last autumn. The fertile eggs were all laid singly or in rows of two or three on the needles of the spruce, and pairing took place quickly or not at all. One female *obeliscata* laid a full complement of eggs within the first three days, and placed them all on the needles, suggesting that she had paired, but all the eggs were infertile. The other infertile females of both species either laid no eggs, or laid comparatively few and after some days delay, and many of the eggs were laid on the sides or bottom of the box, or on the muslin cover. The larvae from the earliest pairing of each cross began to hatch on May 22nd, and at the start thrave on spruce, but after the first and second instars they began to die. The larvae of the *variata* ♂ × *obeliscata* ♀ cross were the hardier and several rapidly outstripped the rest, but of the reciprocal cross only one larva grew with this rapidity. On June 28th I noted that on the whole the larvae of this hybrid were the larger, in spite of the fact that many of the smallest of the larvae of the other hybrid had died.

On July 15th the first imago of each hybrid emerged, but many more *variata* ♂ × *obeliscata* ♀ had pupated than *obeliscata* ♂ × *variata* ♀, and by August 1st, 22 of the former had emerged and only 3 of the latter. In the end even the bigger larvae of both hybrids began to die and I lost two or three which were pupating. On September 21st the last imago, *variata* ♂ × *obeliscata* ♀, emerged, and it was clear that the remaining larvae, which were *obeliscata* ♂ × *variata* ♀, intended to hibernate. Before the end of October they were all dead.

There is no doubt that all the imagines bred are true hybrids. I have mentioned the care taken in the pairing, and to avoid any danger of introducing larvae of either parent species I bred neither *obeliscata* nor *variata*. There was little risk of bringing in larvae on the food-plant. The spruce was gathered from places where *variata* does not occur, and it is not a usual food of *obeliscata*, but nevertheless it was always examined for possible intruders. Luckily most of the larvae grew more quickly than wild larvae of *obeliscata*, and this made my precautions almost unnecessary.

CHARACTERS OF THE HYBRID LARVAE.—In my former paper I pointed out that the larva of *variata* has green legs and that of *obeliscata* pink legs. An examination of the legs of the hybrid larvae in their last instar gave the following results:—*variata* ♂ × *obeliscata* ♀—25 pink: 10 pale pink: 1 green. *Obeliscata* ♂ × *variata* ♀—20 pink: 20 pale pink: 4 almost green: 1 green. Those which I have called almost green showed a faint tinge of pink on every segment, but to the naked eye they appeared green. The leg colour of *obeliscata* is to a great extent dominant over that of *variata* when *obeliscata* is the female parent, but when *variata* is the female parent, the influence of this species is little inferior to that of *obeliscata*.

In my previous paper I showed that most larvae of *obeliscata* had 7 setae on each side of the anal flap and some had 6, whereas in *variata* the majority had 5 and some had 6. In the case of the hybrids there was greater variation. Of 28 hybrid larvae, *variata* ♂

× *obeliscata* ♀, six had 7 on each side, four had 7 on one side and 6 on the other, sixteen had 6 on each side, and two had 6 on one side, and five on the other. Thus ten had more setae than any *variata* I have examined, but only two had fewer than any *obeliscata*, and none had the commonest number in *variata*, 5 on each side. These larvae resembled *obeliscata* more than *variata*. Of 34 hybrid larvae, of *obeliscata* ♂ × *variata* ♀, four had 7 setae on each side, three had 7 on one side and 6 on the other, nineteen had 6 on each side, five had 6 on one side and 5 on the other, two had 5 on each side, and one had 5 on one side and 4 on the other. Seven had more setae than I have found in any *variata*, eight had fewer than I have found in any *obeliscata*, so that in this respect neither species appeared to have a predominating influence in this cross. The number of asymmetrical examples, fifteen out of sixty-two, is rather remarkable and did not seem to be due to injury. It was noticed in some living larvae and in others it was found in the cast skin of the larva after pupation. In one asymmetrical larva of *obeliscata* ♂ × *variata* ♀ the third and fourth setae on the right side were exactly at the same level, one just internal to the other, but in all the others the setae were spaced out fairly evenly along the edge of the anal flap.

The results obtained by examining the setae and the colour of the legs agree. The influence of *obeliscata*, when it is the female parent, is greater than that of *variata*, but, when it is the male parent, it is about equal to that of *variata*.

CHARACTERS OF THE PUPA.—I found that both parent species had pupae varying from pale green to blackish green and was unable to distinguish any difference in the markings or in the structure of the cremaster. The pupae of both hybrids showed the same range of colour variation.

CHARACTERS OF THE IMAGINES.—Hybrid *Thera woodi*, nov. hybr. *T. variata* ♂ × *T. obeliscata* ♀, named after Mr. H Worsley-Wood.

Hybrid *Thera prouti*, nov. hybr. *T. obeliscata* ♂ × *T. variata* ♀, named after Mr. L. B. Prout, whose paper first drew attention to the occurrence of *variata* in England.

Of hybrid *woodi*, 27 were bred, 19 males and 8 females.

Of hybrid *prouti*, 23 were bred, 17 males and 6 females.

It is a pity the different broods were not kept apart both from the point of view of the sex ratios and the colour variation, but the time required for this was greater than I could afford. The excess of males is noteworthy, and I do not think it was due to the death of female larvae. The females on the whole emerged later than the males, but the first *woodi* to emerge was a female and the last to emerge in the case of both hybrids were males. Most of the big larvae which died were, to judge by their size, males and only one was undoubtedly female. It is well known that in some hybrids the sex ratio is abnormal; in some cases there are more males than females and in others all are males.

THE MALES OF HYBRID WOODI.—These fall roughly into four groups.

(a) Four very pale; general effect very smooth and uniform. Two with much more grey than ferruginous both in median area and rest of forewing (Figs. 9 and 10): two with median area pale ferruginous and with ferruginous tint in other parts of wing: one of the latter is less uniform than the other and is paler outside the postmedian and

between the antemedian and basal patch. The shade proximal to the antemedian is faintly indicated in all: the nervures in median area are slightly darkened.

(b) Five rather uniform and lacking in pattern, but darker than the above and with a darker ferruginous median area and basal patch; in four the ground colour of the rest of the wing is much more brown than grey: one is darker than the others and has a browner median area and greyer ground colour (fig. 11): with one exception the shade proximal to the antemedian is very indistinct: nervures in median area are dark.

(c) Seven very pale: pattern variegated like the better marked *variata*, but with pale ferruginous median area and brownish tint in ground colour; postmedian not indented: shade proximal to antemedian well marked: nervures in median area darkened. In five the wing between the postmedian and subterminal from the costa to the bend in the postmedian is much whiter than the rest of the ground colour, a character of *variata* (figs. 12-16).

(d) Three with median area blackish brown: basal patch paler but with very dark edge and dark strips across it; paler lines distal to patch and on either side of median area: ground colour greyish brown. These are indistinguishable from some of the banded forms of *obeliscata* (the nymotypical form) (figs. 17 and 18.)

THE FEMALES OF HYBRID WOODI.—(a) One is pale like the males in group (a), but the ground colour is almost pure grey and the grey shades proximal to the antemedian, and the grey subterminal are very distinct and darker than the pale ferruginous median area itself. The nervures in median area are darkened. (fig. 9.)

(b) One is rather like the males in group (b) but the markings are more distinct. (fig. 22.)

(c) Four are very like the males in group (c) and one is even more prettily variegated; the outline of the postmedian lacks the loops which indent that of *variata*: the nervures in the median area are darkened. (figs. 20 and 21.)

(d) Two are banded, but not so distinctly as the males: the ground colour is a darker brown and the median area is less clearly delimited by pale lines. (figs. 23 and 24.)

MALES OF HYBRID PROUTI.—(a) Four very similar to group (a) of the reverse cross, but with brownish ground colour. (fig. 1.)

(b) Six like group (b) of *woodi*: two with very red-brown ground colour (fig. 2): three with greyer ground like the darkest *woodi*. (fig 3.)

(c) Seven a good deal darker and with one exception not so well marked as group (c) of *woodi*: one has the median area narrow and broken in the way which is so common in *juniperata*. In the figure the median area is too dark. (fig. 4.) But for the more ferruginous median area it might easily be mistaken for the uncommon brown form of *variata*.

All six females of *prouti* correspond with the males of group (c): none show much variation and resemble in pattern the obscurely marked *variata* race *britannica*; in five the ground colour is brown (figs. 6 and 7), and in one grey-brown (fig. 8.)

The two hybrids have many points in common, and their colour and pattern show characters derived from both parents. The median area almost always has the ferruginous or brown colour of *obeliscata*.

The rest of the ground colour varies; in many it is as brown or nearly as brown as in *obeliscata*, but only in two is it nearly as grey as in *variata*. In none is it as pale reddish as in the common var. *herrichi*, and in none as grey as in *variata*. In the majority the pattern is more nearly that of *obeliscata*, although in some it is more like that of *variata*. The outline of the postmedian is almost always that of *obeliscata*, and only in one is it as looped as in *variata*. The darkening of the nervures in the median area is well marked in most, and in this respect they are more like *variata*. The banded forms are almost identical with some *obeliscata*. The chief differences between the two hybrids are that *prouti* is the darker and lacks the branded and pale variegated forms.

Taking all the hybrids together, there are several specimens which would attract little or no attention in a series of *obeliscata*, but none would be mistaken for *variata*, although one at least is more like this species. The effects attributable to each parent are less easy to assess exactly in the case of the imagines than in the larvae, but here too the influence of *obeliscata* appears to be the greater especially when it is the female parent. Those most like *obeliscata* occur amongst the *woodi* and the one most like *variata* amongst the *prouti*.

Owing to its much more restricted distribution on the continent Herr Höfer thinks it probable that *obeliscata* is the more recent species, or, to be more accurate, he regards it as a species in the making, but he expresses the view that crossing it with *variata* may lead to a more definite conclusion. This has now been done, but it would have been still more interesting to have seen to what extent segregation of characters occurred in the second generation of the hybrids and whether *obeliscata* would have proved to be a true dominant. No attempt was made to do this, because I have found it impossible to keep *Thera* larvae alive through the winter, and I do not even know whether such secondary hybrids can be obtained.

In the case of hybrids the species with the greater influence on the offspring is usually regarded as the older, and if this be accepted as true, *obeliscata* must be phylogenetically older than *variata*. The result is unexpected, but I am very doubtful if the argument is sound. It seems to me more probable that the recessive is the older form. Recessive characters must be common to both species, but dominant ones may be present only in one. If they have not been lost by the species lacking them they must have been newly acquired, and indicate that the species possessing them is the younger.

Bowater describing his hybrid *Cerura furecula* ♂ × *bicuspis* ♀ says that it shows a greater resemblance to *furecula* than to *bicuspis* and gives the following quotation from Harrison. "The superior influence of the male is noted in practically all the hybrids I have reared, not only amongst the genus *Nyssia* and *Lycia*, but also in Ennomids and Larentiids likewise." The hybrid *woodi* is an exception to this rule, for both on the larvae and imagines the female parent has the superior influence.
